A specimen of *Parvicuculus* Harrison & Walker 1977 (Aves: Parvicuculidae) from the early Eocene of France

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The fossil species *Parvicuculus minor* was described by Harrison & Walker (1977) from the early Eocene London Clay deposits in England, and was hitherto known only from an incomplete tarsometatarsus. As indicated by its name, *Parvicuculus* was considered a member of the Cuculidae (cuckoos) by Harrison & Walker (1977).

Cuculiform affinities of *Parvicuculus* were, however, disputed by Olson & Feduccia (1979), who instead assumed the taxon to be a member of the Eocene coraciiform Primobucconidae (Houde & Olson 1989, Mayr *et al.* 2004), in particular they considered a relationship to the alleged primobucconid '*Neanis*' *kistneri* Feduccia 1973 to be possible. Harrison (1982) reevaluated the phylogenetic affinities of *Parvicuculus* and again considered it a member of the Cuculiformes, albeit not within the Cuculidae but in the new taxon Parvicuculidae. Assignment of *Parvicuculus* to the Cuculiformes was subsequently questioned by Martin & Mengel (1984) and Baird & Vickers-Rich (1997); the taxon was placed in Aves *incertae sedis* by Mlíkovský (2002).

Here we report on a second specimen of *Parvicuculus* from the early Eocene of Condé-en-Brie in France. The new specimen is an incomplete tarsometatarsus that exhibits almost the same state of preservation as the holotype of *Parvicuculus minor*. It is the second bird specimen described from Condé-en-Brie, in addition to a tarsometatarsus of the Primobucconidae (Mayr *et al.* 2004). The age of the French locality is the same as that of Burnham-on-Crouch, the type locality of *P. minor* (Mammalian Paleogene 8–9, i.e. *c.*52 million years ago; Mlíkovský 1996, Legendre & Lévêque 1997).

Material and methods

Osteological terminology follows Baumel & Witmer (1993), whilst measurements are in mm and represent the maximum length of the bone along its longitudinal axis. SEM photographs of sections of the French fossil were digitally composed to show the complete bone. The fossil specimens are deposited in the Muséum national d'Histoire Naturelle, Paris, France (MNHN), and the National Museum of Natural History, Washington, USA (USNM).

Systematic paleontology

Parvicuculidae Harrison 1982

Emended diagnosis

Small birds that are characterised by: (1) tarsometatarsus short and stout, (2) with medially situated tuberositas musculi tibialis cranialis, (3) deep fossa infracotylaris

dorsalis, (4) well-developed crista medianoplantaris, (5) large foramen vasculare distale, (6) foramen interosseus distalis, and (7) trochlea metatarsi IV with plantarly projecting wing-like flange.

Remarks

Harrison (1982) also included *Procuculus minutus* Harrison & Walker 1977 in the Parvicuculidae and partially based his diagnosis of the latter on this species. However, as already noted by Olson & Feduccia (1979), there is no indication that *P. minutus* is in any way closely related to the Parvicuculidae and we thus present a diagnosis of the taxon based on the type genus *Parvicuculus* alone.

Of the above characters, (1)–(4) are here considered to be derived within Neornithes, as they are absent in presumably basal representatives of this taxon, such as palaeognathous birds and Galloanseres (e.g. Mayr & Clarke 2003).

Parvicuculus Harrison & Walker 1977
Parvicuculus cf. *minor* Harrison & Walker 1977

Referred specimen

MNHN-CB-17345 (left tarsometatarsus lacking the trochlea metatarsi II; Figs. 1A–C, 2A, B).

Locality and horizon

Condé-en-Brie, France (collection Louis); early Eocene, MP 8–9 (Schmidt-Kittler 1987).

Measurements (with dimensions of the holotype *P. minor*, after Harrison & Walker 1977)

Length, 10.5 [11.7]; mediolateral width of trochlea metatarsi III, 1.3 [1.5].

Description and comparison

The short and relatively stout bone is of similar proportions to the tarsometatarsus of the extant Tawny Frogmouth *Podargus strigoides* (Podargidae, Fig. 2D), from which it, however, differs in osteological details. On the proximal end, the eminentia intercondylaris is very low, and the cotylae lateralis et medialis are sloping laterally and medially respectively, thus giving the proximal end a rounded appearance (Fig. 2A), which is further strengthened by the fact that this end is quite damaged and abraded. Two foramina vascularia proximalia are present, situated in a deep fossa infracotylaris dorsalis (Fig. 2A); the lateral foramen vasculare proximale is smaller than the medial one. The tuberositas musculi tibialis cranialis is situated at the medial margin of the bone. There is a well-developed crista medianoplantaris and the fossa parahypotarsalis medialis is more marked than the fossa parahypotarsalis lateralis. The hypotarsus is broken. The foramen vasculare distale on the distal end of the bone is very large, the osseous bridge separating it from the

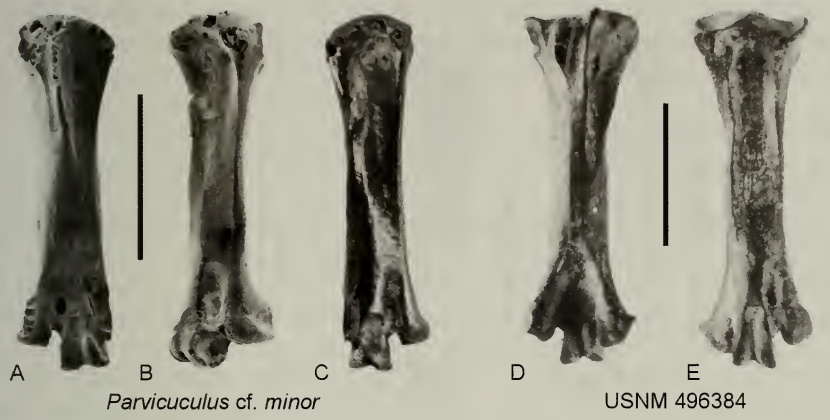

Figure 1. *Parvicuculus* cf. *minor* Harrison & Walker 1977, referred specimen MNHN-CB-17345 from the early Eocene of Condé-en-Brie, France, in plantar (A), dorsolateral (B), and dorsal (C) views, in comparison to the plantar (D) and dorsal (E) aspect of a tarsometatarsus from the early Eocene Nanjemoy Formation, North America (specimen USNM 496384, reversed to facilitate comparisons; from Olson 1999, with permission of the author). A and B are SEM photographs, C is a picture of the sputtered specimen (which originally was white). Scale bars = 5 mm.

incisura intertrochlearis lateralis narrow. Contrary to the Primobucconidae (Mayr *et al.* 2004) and modern rollers *Coracias*, there is a foramen interosseus distalis (Fig. 2B). The fossa metatarsi I is situated at the beginning of the distal third of the bone. The trochlea metatarsi IV is much shorter than the trochlea metatarsi III, somewhat laterally splayed, and bears an elongated, plantarly projecting wing-like flange. The trochlea metatarsi III is approximately as long as it is wide, on the plantar surface the lateral rim reaches slightly farther proximad than the medial one. The trochlea metatarsi II is broken but the remaining parts indicate that it was more plantarly deflected than the trochlea metatarsi IV.

Discussion

Although specimen MNHN-CB-17345 is slightly smaller than the holotype of *Parvicuculus minor*, the size difference may be due to individual variation. We tentatively assign it to *P. minor* Harrison & Walker 1977, as it does not exhibit significant morphological differences from that species.

As noted by Olson & Feduccia (1979) and Baird & Vickers-Rich (1997), the tarsometatarsus of *Parvicuculus* is very different from that of the Musophagidae and Cuculidae. Harrison & Walker (1977) did not list any characters supporting their classification, and Harrison (1982) also failed to present derived characters that support this assignment. The tarsometatarsus of *Parvicuculus* differs from that of the Primobucconidae *sensu stricto* (i.e. the genus *Primobucco*) and all other coraciiform birds in being proportionally more abbreviated and in the plesiomorphic

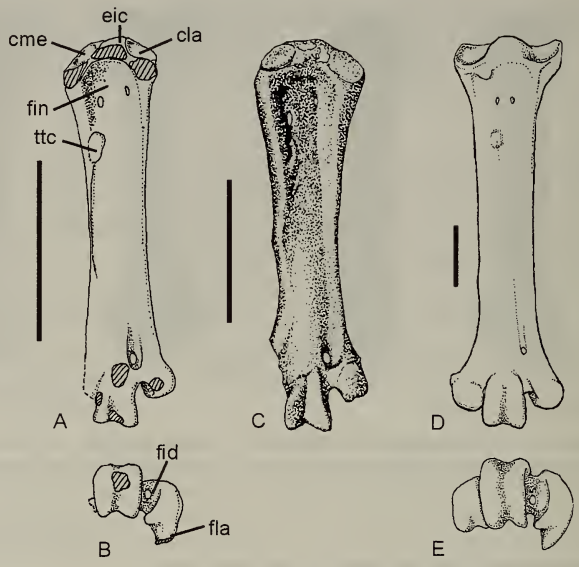

Figure 2. *Parvicuculus* cf. *minor* Harrison & Walker 1977, tarsometatarsus of specimen MNHN-CB-17345 in dorsal (A) and distal (B) views, in comparison to the corresponding bone of (C), the holotype of *Parvicuculus minor* (from Harrison 1982), and (D, E), modern *Podargus strigoides* (Podargidae). Abbreviations: cme—cotyla medialis; cla—cotyla lateralis; eic—eminentia intercondylaris; fid—foramen interosseus distalis; fin—fossa infracotylaris dorsalis; fla—wing-like flange on trochlea metatarsi IV; ttc—tuberositas musculi tibialis cranialis. Scale bars = 5 mm.

(Mayr & Clarke 2003) presence of a foramen interosseus distalis (the canal opening into that foramen is plantarly open in the Primobucconidae: see Mayr *et al.* 2004). '*Neanis*' *kistneri* is known from a flattened skeleton on a slab and its tarsometatarsus cannot be compared in detail with that of *Parvicuculus*. However, '*N.*' *kistneri* clearly had a fully zygodactyl foot, i.e. the fourth toe was permanently retroverted (Feduccia 1973), for which the arrangement of the metatarsal trochleae shows no indication in *Parvicuculus*.

There are several other early Eocene avian taxa with a greatly abbreviated and stout tarsometatarsus bearing a superficial similarity to that of *Parvicuculus*, all of which are, however, clearly distinguished in osteological details. *Parvicuculus* differs from *Pumiliornis tessellatus* Mayr 1999a (Aves *incertae sedis*, Mayr 1999a), *Paraprefica* Mayr 1999b (Nyctibiidae, Mayr 1999b, 2001), and *Palaeopsittacus* Harrison 1982 (Aves *incertae sedis*, Mayr 2003) in the presence of a well-developed crista medianoplantaris and the larger foramen vasculare distale. In addition, the tarsometatarsus of *Parvicuculus* is stouter than that of *Palaeopsittacus* (ratio max. length/min. mediolateral width of shaft is 5.7 mm in *Parvicuculus* vs 6.8 mm in *Palaeopsittacus*), with a deeper furrow of the trochlea metatarsi III, but less stout than that of *Paraprefica* (ratio max. length/min. mediolateral width of shaft is

5.7 mm in *Parvicuculus* vs 4.7 mm in *Paraprefica*). Detailed comparisons with *Fluvioviridavis* Mayr & Daniels 2001 (Aves *incertae sedis*) are impossible, owing to the poor preservation of the tarsometatarsus in the single known specimen of the latter taxon (see Mayr & Daniels 2001).

The tarsometatarsus of *Parvicuculus* closely resembles, however, a complete tarsometatarsus from the early Eocene of the North American Nanjemoy Formation (specimen USNM 496384), that was assigned to the apodiform Aegialornithidae by Olson (1999), but has not been compared with *Parvicuculus*. Differences from *Parvicuculus* mainly concern the proportions of the bone, which is slightly stouter in *Parvicuculus*, and the size of the foramen vasculare distale, which is larger in *Parvicuculus* (Figs. 1D, E). As noted by Olson (1999), the Nanjemoy tarsometatarsus is more abbreviated than the corresponding bone of the Aegialornithidae (see Mourer-Chauviré 1988: pl. 1), and we consider it likely that it belongs to a member of the Parvicuculidae. It further differs from the tarsometatarsus of the Aegialornithidae in that there are plantarly open furrows on the hypotarsus, instead of a closed canal. Additional skeletal elements are required for a definitive phylogenetic placement of the Parvicuculidae, although tarsometatarsal morphology of this taxon does not conflict with a position within or close to the Cypselomorphae *sensu* Mayr (2002), i.e. a clade including Caprimulgidae (nightjars), Nyctibiidae (potoos) and apodiform birds (swifts and hummingbirds). As exemplified by the complete Nanjemoy specimen, the Parvicuculidae agree with modern Steatornithidae (oilbird) in the shape of the trochlea metatarsi III and the presence of a plantarly open furrow on the hypotarsus. The Oilbird *Steatornis caripensis* also has a greatly abbreviated tarsometatarsus which otherwise, however, strongly differs from that of *Parvicuculus* in many osteological details, including absence of a crista medianoplantaris and the arrangement of the trochleae (Mayr 1999b: fig. 11).

Independent of its precise phylogenetic affinities, the specimen described in this study is of interest, as it is not only one of the very few avian records from the early Eocene of France, but also provides evidence for the existence of a previously unrecognised distinctive group of birds that appears to have been widespread in the early Eocene of the Northern Hemisphere.

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